

December 15, 2006

Donald L. DeAngelis, Editor
The American Naturalist
1427 E. 60th St.
Chicago, IL 60637

MS #41465, version 1

Dear Dr. DeAngelis,

This letter accompanies a revised version of MS #41465, "Habitat Connectivity and Ecosystem Productivity: Implications from a Simple Model". The paper has been revised substantially, following the detailed guidelines provided by you, Associate Editor Grover and two referees. Those comments and guidelines are highlighted below in yellow, and each is followed by a description of how the analyses and text have been modified.

Editor Donald L. DeAngelis:

Your paper is not well organized, and the model description is too lengthy at present. The construction and results of the one-habitat NPZ model should go into an online appendix. The description of the two-habitat model should go into a brief "Model Formulation" section. ... the "Results" and "Discussion" sections should be separated ... keep your main text down to about 19 or 20 pages

I followed, almost exactly, the suggestions by James Grover to reorganize this manuscript. All details of model construction, one-habitat NPZ simulations, and process equations and parameters have been excised from the manuscript and placed in two appendices. A new section "Model Formulation and Hypothesis Testing" presents the general structure of the two-habitat model and explains how simulation experiments are used to test the null hypothesis presented in the Introduction. Separate "Results" and "Discussion" sections have been created, following Dr. Grover's guidelines. The manuscript comprises 18 pages of text and figures (within your target length); the appendices and references comprise an additional 9 pages.

Associate Editor Dr. James P. Grover:

To be convinced that the paper has sufficient broad appeal for American Naturalist, I think that major revisions need to be made. The main themes don't stand out well, mostly due to presentation issues that can be fixed with reorganization. Perhaps more difficult is what seems to me to be a questionable assumption (as explained below).

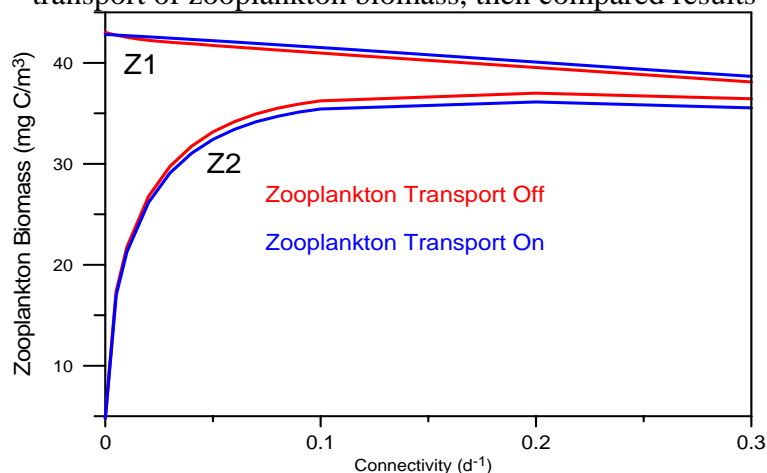
I suggest the following changes in organization to the authors. Put the construction and results of the one-habitat NPZ model into an appendix. A new section on "Model Formulation" should present the two-habitat coupled model, equations (24) - (26), with explanations focusing on the parameterization of transport terms (eqs. 21 - 23), and those terms that couple N, P, and Z. Put the details of temperature- and light-dependence in another appendix, along with other parameterization issues (eqs. 7 - 10). The presentation of the spatially coupled NPZ model can say that zero connectance is the special case of isolated food chains, but leave the details of

these in appendices. I also suggest separating “Results” from “Discussion”. With the material on the results of the one-habitat NPZ model put into an appendix, the central results on connectivity (Figs. 3-5) would be the only thing to present in the results section, better emphasizing the paper’s contribution. The discussion could then focus on generalizing the results by way of the C/PG principle and related issues.

As explained above, the revised manuscript includes these suggested changes in format and organization. I believe the primary results of this study and their significance are more clearly highlighted, and the paper is more accessible for a general reader.

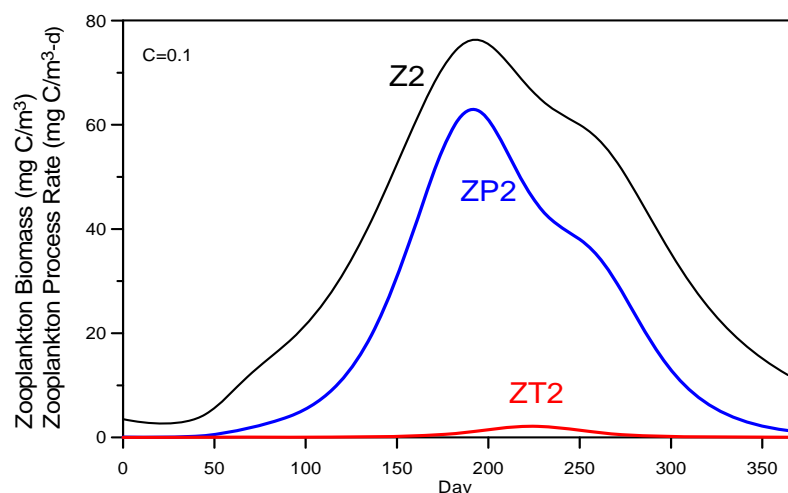
Assumption that I'm worried about: In the spatially coupled formulation, N and P are transported between sub-habitats but not Z. .. I don't see a strong rationale for this assumption, and I would like some assurance that the main results are robust to relaxing it, and going with what seems to me to be the more natural assumption that Z is transported along with N and P. Alternatively, can the author present a convincing explanation that there's a good biological reason for this assumption?

Crustacean zooplankton are not transported as passive particles because they can swim and have behavior. Cladocerans migrate laterally between shallow littoral zones during daylight (to avoid predation) and to open pelagic habitats during dark (to feed). Copepods have vertical migration behavior phased with tidal currents to maintain their longitudinal position along estuarine salinity gradients. However, this behavior doesn’t help guide the treatment of zooplankton transport in a two-box model. So, in response to this comment I revised the model to include dispersive transport of zooplankton biomass, then compared results with the original model formulation in



which zooplankton transport was assumed to be zero. This figure shows results as originally presented in Figure 3c (red curves), compared to simulations with zooplankton transport added (blue lines). Simulated mean annual zooplankton biomass is insensitive to the addition of Z transport. This was a bit surprising, and the following figure provides an explanation:

This figure shows an annual simulation of zooplankton biomass in the recipient habitat, Z2 (black line), for connectivity $C=0.1$. The blue line shows simulated daily zooplankton production and the red line shows simulated daily zooplankton transport. This experiment reveals that the rate of



biomass transport is much smaller than the rate of biomass production, explaining why model results are insensitive to the addition or inclusion of zooplankton transport. In response to Dr. Grover's understandable concern about the implications of excluding a zooplankton transport process, I re-ran all simulations with zooplankton transport treated identically to the transport of P and N. This modification of the model did not lead to altered conclusions about the implications of connectivity strength, but it is based on a consistent treatment of NPZ dynamics.

C/PG: I really like the suggestion that C/PG is a dimensionless number governing when coupling like this enhances total production. But I think this suggestion needs more emphasis, and could be used to make generalizations. As one referee suggests, there might be enough literature to tentatively identify ecosystems and circumstance where $C/PG > < = 1$. The components of this number are commonly measured (spatial coupling like this has been widely used in engineering models of water quality, so there's a lot of parameterization information related to C available, and PG is a classic subject of aquatic ecology). I think a paragraph or two along these lines would raise the general appeal of the paper.

In response to this comment, and a comment from Reviewer 1 below, I conducted a new set of simulation experiments to explore the robustness of the functional relationship between system productivity and the ratio C/PG. These results are presented in a new Figure 5, and they are discussed in a section of the Discussion "Scaling Rules of Pelagic Ecosystem Productivity". I included a new simulation of time-variable nutrient influx, such as a system that receives river pulses of nutrients. I ran a second new simulation in which the habitats are only seasonally connected, such as a river-floodplain system. Then I ran simulations in which the connectivity rate was modified by daily fluctuations in: wind stress to depict exchange between a lake's littoral and open pelagic habitat; tidal currents that drive mixing across bathymetric gradients of estuaries; and river inflow to depict a fluvial system in which connectivity varies with discharge. Results show that inclusion of a continuing nutrient source amplifies overall system production, intermittency of connectivity decreases overall system production, and daily changes in wind-, tidal-, or river-driven connectivity have little effect on system production. However for each simulation, regardless of nutrient supply or the treatment of time-variable connectivity, the model results showed the same functional form between connectivity rate and system primary and secondary productivity. In each simulation, optimum system productivity occurred when the nondimensional number C/PG_1 approached one. These new simulations add confidence that this primary model result is robust and that system production is influenced by the balance between rates of transport and biological production. A mechanistic explanation of this outcome is included now in the Discussion.

Minor comment: Fig. 4, please define line types in the legend.

Done

REVIEW 1

the author only focused on the linkage between shallow and deep pelagic habitats. Is this the most important linkage? And what would be the outcome of the modeling exercise if one would include an additional linkage (e.g. estuary-river)? And how does the coupling change with nutrient pulses as a consequence of flood pulses and season?

The simulation experiments were not designed to link a shallow and deep habitat, but rather to link habitats that provide distinct functions – in this case net autotrophy (organic carbon source) and net heterotrophy (regenerated nutrient source). These differences were created with simulations of a shallow (high light) and deep (low light) pelagic habitat. But the intent here is to explore the system dynamics as a function of habitat connectivity where the system is a composed of functionally variable habitats. I hope this important point is clearer now to readers after inclusion of new simulation experiments (see above) to depict a range of linked hydraulic systems such as rivers and flood plains, subtidal and intertidal estuarine habitats, open channels and lateral recirculation zones of rivers, and lake littoral and pelagic habitats. In response to this comment, the revised manuscript includes a simulation of nutrient pulses and, as explained above, the same connectivity-productivity relationship was observed.

Page 2, line 5: It is stated that the spatial connectivity is viewed as a zero sum process. However, in the introduction, something different is said (page 4, lines 2-8). There, the author says that it is not clear. In addition, stream-hyporheic exchange processes enhance the production in both systems, primary in the water column and secondary in the hyporheic.

I removed these sections of text that were contradictory.

p.3 L.10: “.... and the earth sciences (Rougharden et al. 1988)”. It is not clear how earth sciences should be integrated into this model.

I removed this sentence.

p. 6, L.7: Is nitrogen the key limiting nutrient? What is with other nutrients such as silica and P? Damming of the tributaries might modify the silica concentration, therefore altering the Si:N ratio and the composition of the phytoplankton (shift from a diatom to a blue-green algae community). How sensitive is the model for differences in planktonic community composition?

There's a lot in this question/comment. Decades of nutrient analyses in the Sacramento-San Joaquin Delta show that this water body is highly enriched in both N and P (Jassby et al. 2002). Only rarely have DIN and DRP fallen to levels that might limit phytoplankton growth, and these events have always been short-lived. Historically, there has been an equal number of occurrences of DIN and DRP reaching limiting concentrations. I used nitrogen in the NPZ model as a generic representation of any macronutrient that can limit phytoplankton growth. If P was used as the limiting nutrient, with appropriate half saturation constant for phytoplankton growth, the simulation results would have been unchanged. In particular, the primary result of a nonlinear relationship between habitat connectivity and ecosystem productivity holds, regardless of the limiting nutrient. Dissolved silicate concentrations are always very high in this system (typically above 100 micromolar), and they never approach concentrations that limit diatom growth. The phytoplankton community is dominated by taxa of high food value to consumers – diatoms and cryptophytes (Lopez et al. 2006). The reviewer's question of how changes in phytoplankton taxonomic composition would alter model results is certainly important. However, this problem of variable food quality is a separate issue that would ideally be addressed following this study that addressed the problem of variable food quantity for consumers.

- Page 6, lines 10-12. Here the author describes the system, but a lot of basic information on the system is missing. Maybe a clear differentiation between methods, results and discussion might help.

This has been done, as explained above.

- Page 14, plot 3. Why is P of the shallow section not affected by nutrient depletion? It seems that there is an effect of the nutrient concentration on P, but P is always really high through nearly all the year. If P is mainly a result of phytoplankton development, then the changes are really much faster than the model says. I mean, nutrients can be rapidly depleted during a boom, and then there is a decline in the phytoplankton.

The treatment of nutrient regeneration in the original model was overly simplistic and built from the assumption that all nutrients flowing into predator biomass are instantaneously and completely returned to the pool of dissolved nutrients. This created a seasonal equilibrium condition that sustained high, near constant, phytoplankton biomass in the shallow habitat. These high-biomass steady-state events occur in nature – e.g., brown tides in high-nutrient shallow coastal lagoons that persist for months or years. However, the original description of nutrient regeneration was grounded in an assumption that is difficult to justify. So, in response to Reviewer 2's comment (see below), I modified the model with a more realistic approximation of nutrient regeneration. This alteration of the model led to elimination of the steady-state high biomass and a seasonal decline of phytoplankton biomass after the spring bloom (see fig. 2b).

- Page 20, line 21. Although resource fluxes are not commonly measured in aquatic ecosystem studies . . . I am not of the same opinion since there are a lot of papers that attempt the relationship between channels, riparian zones, and floodplains.

I removed this statement from the text.

Figures 2, 3, 4: Legends for y-axes should be added or expanded.

Done

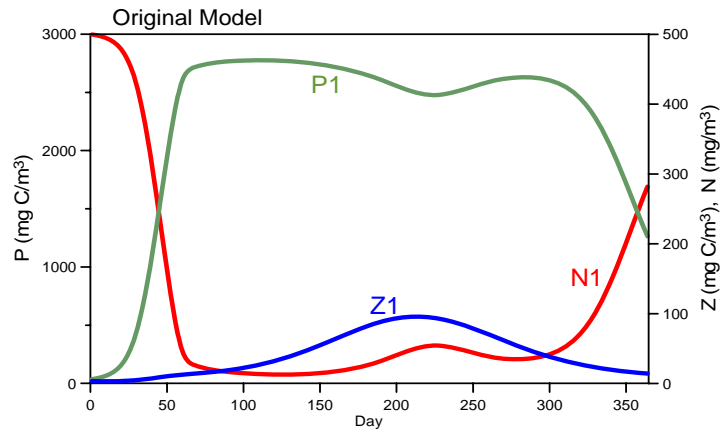
Figure 5: Units (Z and PTransport)?

These have been added.

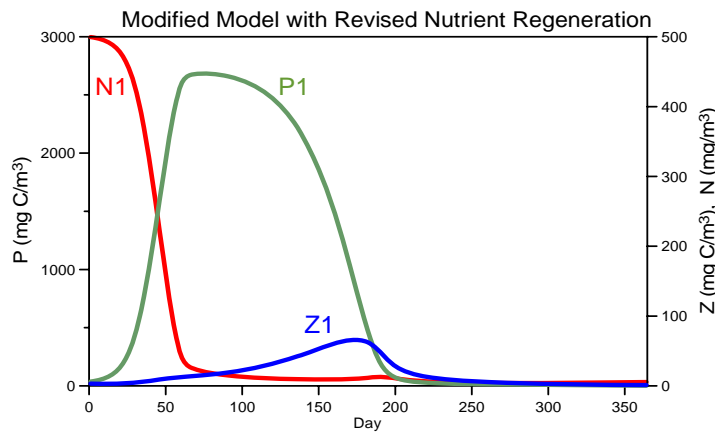
REVIEW 2

on P8 line 25:26 & p9 line 1:2, you state that all zooplankton mortality is from predation by higher trophic levels. Please justify further your model formulation/assumption that this material is immediately recycled to regenerated nutrient. What would happen in your system if most of this material was exported to higher trophic levels?

The figure below provides an answer to this question. The top panel shows simulated annual N, P and Z in the shallow donor habitat for $C=0$ (to remove effects of transport), using the original model formulation in which the N content of predator biomass is regenerated completely and instantaneously. The bottom panel shows the same simulation after the model was modified to retain that N content within predator biomass, assuming a 29% growth efficiency of planktivorous fish. As anticipated by Reviewer 2, this modification of nutrient regeneration has a large effect on simulated NPZ dynamics because the system drains the pool of N as it is converted into biomass of primary, secondary and tertiary producers. This approach is a more realistic approximation of the coupling between production processes and nutrient regeneration, so the revised manuscript presents results of simulations with the modification suggested by Reviewer 2. Although this revised treatment of regeneration does have a big influence on annual



NPZ dynamics, it does not change the primary result of the simulations presented here: system N regeneration and P and Z production still follow an asymptotic functional response to C, attaining optima at $C/PG_1 \sim 1$.



P 19 line 3 doesn't make sense - I think you missed out a word.

Yes, this has been corrected

In summary, the NPZ model has been modified to include zooplankton transport and a more realistic treatment of nutrient regeneration from secondary consumers. Additional simulations were run to test the generality of model results and represent time variable connectivity and nutrient influx. Model details, of interest primarily to specialists, have been placed in appendices, and the streamlined paper focuses on new results and their ecological significance.

Thank you for your consideration of this revised manuscript.

Sincerely,

James E. Cloern